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REPRODUCTION, EMBRYONIC ENERGETICS, AND THE MATERNAL-FETAL RELATIONSHIP IN THE VIVIPAROUS GENUS *SEBASTES* (PISCES: SCORPAENIDAE)

GEORGE W. BOEHLERT* AND MARY M. YOKLAVICH

College of Oceanography and Marine Science Center, Oregon State University, Newport, Oregon 97365

ABSTRACT

Reproduction in the scorpaenid genus *Sebastes* has been characterized as primitive ovoviviparity. In the black rockfish, *S. melanops*, egg size is small (0.8 mm), but the gestation period is 37 days and larvae at birth are well developed, with a remnant of yolk and the ability to initiate feeding. To test the hypothesis that this species is viviparous with additional maternal nutrition, we studied embryonic energetics and morphology. Catabolism during development utilized 64% of the yolk energy, resulting in a maximum yolk utilization efficiency of 36%, similar to oviparous fishes. Calorimetry, however, demonstrates that 81% of the initial yolk energy is present at birth. Thus approximately 70% of the catabolic energy is contributed by the maternal system during gestation. Microscopic analysis of embryonic epidermis suggests no specializations for nutrient uptake. Histological observations, however, reveal that the hindgut is functional approximately 22–25 days after fertilization. Thus, we suggest that nutrition occurs through consumption and assimilation of ovarian fluid.

Reproductive modes in the Scorpaenidae have apparently evolved from simple oviparity in seven of eight subfamilies, to lecithotrophic viviparity in more primitive members of the subfamily Sebastinae, through matrotrophic viviparity in *Sebastes*. This pattern involved progressively longer retention of embryos until after organogenesis and functional differentiation of the gut, facilitating this rather primitive form of embryonic nutrition among matrotrophic viviparous species.

INTRODUCTION

Reproductive modes in the teleost fishes historically have been grouped into the categories oviparity, ovoviviparity, and viviparity. Oviparous species shed gametes from the body and fertilization and embryonic development are external. In ovoviviparity and viviparity [referred to herein as lecithotrophic and matrotrophic viviparity, respectively, after Wourms (1981)], fertilization is internal and development proceeds within the female reproductive system. The evolution of these reproductive modes involved a compromise between high reproductive rates with low survival and low reproductive rates with high survival. The former is exemplified in the oviparous fishes, the latter in viviparous fishes, although variations exist within each mode of reproduction. The traditional differences between lecithotrophic and matrotrophic viviparity involve the provision of maternal nutrition after oogenesis; it is lacking in strictly lecithotrophic viviparous species. There is a continuum of levels of maternal nutrition in matrotrophic viviparous fishes, but in most species the actual maternal-fetal relationships during gestation are unknown (Wourms, 1981). The coelacanth

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* Present address: Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, Honolulu, Hawaii 96812.

Latimeria, for example, was described as a lecithotrophic viviparous species by Smith *et al.* (1975), but was later shown to be a matrotrophe despite a lack of specialized structures for nutrient uptake (Wourms *et al.,* 1980). Further research on the maternal-fetal relationship will help us understand the evolution of viviparity in fishes (Wourms, 1981).

In the family Scorpaenidae, live-bearing is present in the subfamily Sebastinae. The most advanced genus, *Sebastes,* has a center of distribution in the North Pacific and is comprised of some 106 species worldwide (Barsukov, 1981). Reproduction in this genus is considered to be primitive among viviparous species, with no maternal nutrition (Wourms and Cohen, 1975; Wourms, 1981). Fecundity approaches that of the most highly fecund oviparous species, with individual fecundity to 2,300,000 in *S. paucispinis* (Phillips, 1964) and weight specific fecundity reaching 500 eggs per gram body weight (MacGregor, 1970; Boehlert *et al.,* 1982). Egg sizes range from about 0.7 to 1.5 mm, the gestation period is approximately 1–2 months long, and larval size at birth is relatively small, ranging from 4 to 9 mm (Fujita, 1957; Moser *et al.,* 1977). The larvae are relatively well developed, however, and are generally born at a developmental stage with organogenesis complete, jaws developed, and the ability to initiate feeding. Moser and Butler (1981), in an attempt to rear larvae of *S. dalli,* suggested that the lack of success in rearing *Sebastes* larvae may be related to the timing of birth; larvae in the wild are well developed at birth whereas those used in laboratory rearing are typically born prematurely. They speculated that additional maternal nutrition might be critical to complete organogenesis late in gestation. To test the hypothesis that reproduction in *Sebastes* is matrotrophic viviparity, we describe the energetics and nutrition of embryonic black rockfish, *S. melanops,* during gestation.

Materials and Methods

Experimental animals

Sebastes melanops is a fairly shallow-living rockfish, generally inhabiting waters from 8 to 55 m (Barsukov, 1981); adults inhabit nearshore rocky reefs from Baja California to the Aleutian Islands (Hart, 1973). All females are mature at an age of 9 years and a length of about 43 cm off Oregon (McClure, 1982), and give birth predominantly during January through March (Laroche and Richardson, 1980). Larvae are pelagic, as is typical of *Sebastes* (Ahlstrom, 1961), and emigrate to nearshore, intertidal, and estuarine areas at ages from 4 to 6 months (Boehlert and Yoklavich, 1983).

Adult *S. melanops* were collected on 8–9 January 1982 by hook and line from a sport fishing vessel off Seal Rock, Oregon in 10–20 m of water. Excess swim bladder gas was removed with hypodermic needles. Fish were held in large circular tanks (1.2 m diameter, 700-liter capacity) supplied with circulating sea water at 10°C (±1°C) during experiments. Following a 2-week period of adjustment to laboratory conditions, sex and stage of ovarian development were determined by catheterization and gentle suction; fish were tagged and segregated on the basis of reproductive state. Of the 16 females, 8 were gravid with embryos at various stages of development, 3 were preovulatory, and 5 were either immature or spent. The females with developing embryos were individually isolated in small circular tanks (0.7 m diameter, 120-liter capacity). Over time, despite separation from males, the three preovulatory females ovulated. The ova were fertilized, and subsequently underwent embryonic development. This is evidence of sperm storage since, in many species of *Sebastes,* insemination occurs up to six months prior to fertilization (Sorokin, 1961; Moser, 1967a).

Developing embryos were obtained by extracting ovarian samples from the 11 ripe females on a weekly basis from 22 January 1982 until parturition. Adult fish were anesthetized with tricaine methanesulfonate (MS-222; 75 mg/liter sea water) and catheterized using a sterile glass pipette. Oppenheimer's (1937) classification of developmental stages of *Fundulus heteroclitus* and Moser's (1967a) description of *S. paucispinis* development were used to identify stages of *S. melanops* embryos. Following Moser (1967a) and Shimizu and Yamada (1980), Oppenheimer's (1937) stages through stage 32 were found adequate for description of *Sebastes* development. Samples from different females from unfertilized eggs to extruded larvae, were taken for estimates of dry weight, ash, carbon and nitrogen, and for measurements of oxygen consumption. Examination of egg diameter from six different females revealed little variation, with mean 0.83 mm (standard deviation 0.026) and range 0.80–0.87 mm.

Calorimetry, nitrogen, and protein analysis

The maternal nutritional contribution to embryonic development was analyzed using bioenergetics and nitrogen and protein budgets. Calorimetry was used to estimate the energy content of developing embryos at eight stages, from unfertilized eggs to extruded larvae. After catheterization of gestating embryos, dry weights were measured to the nearest μg on a Perkin-Elmer AD-2Z microbalance. Groups of embryos were dried to a constant weight at 60°C. Ash content was determined after 3 hours combustion in a muffle furnace at 500°C. Samples were analyzed for carbon and nitrogen content using a Perkin-Elmer model 240-B carbon-hydrogen-nitrogen analyzer. The nitrogen-corrected equation from Salonen *et al.* (1976) was used to convert percent carbon to calories as follows:

$$\text{cal/embryo} = ([0.65\ (\%C) - 12.237]239)\ W$$

where C is carbon content per ash-free dry weight (AFDW) of sample and W is the AFDW of the embryo. While this method is based upon invertebrates, the estimated energy content of unfertilized yolk (6281 cal/g AFDW) is within the ranges of caloric estimates for marine fish eggs as summarized by Robertson (1974). Further, this relationship appears to hold for a diverse group of taxa, including phytoplankton and marine and freshwater protozoa (Finlay and Uhlig, 1981).

From additional specimens collected in 1984, protein content was determined for four developmental stages using the microbiuret method of Itzhaki and Gill (1964). Bovine serum albumin was used as a protein standard. The same specimens were analyzed for CHN content for comparison with 1982 specimens and to determine the percentage of protein nitrogen. This latter value was determined by dividing protein by 6.25.

Oxygen consumption

We measured respiration rates to compare the energy content of the developing embryos with the catabolic energy required during gestation. Embryos were removed by catheterization and placed in physiological saline (Forster and Hong, 1958) isosmotic with ovarian fluid (*ca.* 325 mOsM/kg, determined in a Wescor vapor pressure osmometer) in 15 ml respiration flasks. Experiments were performed in darkness at 10°C in a Gilson differential respirometer following standard techniques (Umbreit *et al.*, 1972). Embryos in respirometers were allowed to equilibrate for 0.5–1 hour prior to initial readings; subsequent readings were taken every 1–2 hours for 5–10 hours. Most experiments were performed with three replicates. Numbers and dry

weights of embryos per vessel were determined upon completion of experiments and results were expressed as μl O_2/embryo/h and μl O_2/mg AFDW/h.

One of the problems in determining the total embryonic oxygen consumption during gestation is that *Sebastes* is viviparous; it is therefore difficult to establish a zero time for fertilization. Length of time spent at each stage of development was determined from samples of embryos taken by successively catheterizing females during gestation, at approximately weekly intervals. By determining the change in stage over the interval, we were able to estimate the duration of each Oppenheimer stage at 10°C. Using these estimates, we integrated the time spent at all stages to calculate a gestation period and also to estimate the total oxygen consumption during the gestation period. We felt that this estimate would be based upon the maximum number of females and would minimize individual variability.

Morphology

Histology of the alimentary tract and the surface structure of the epidermis were examined to determine the site of energy uptake in the developing embryos. For histological examination, small groups of catheterized embryos were preserved in isosmotic buffered 2% glutaraldehyde. Embryos were imbedded in acrylic resin (LR White), sectioned at 2 μm, and stained in hematoxylin and methylene blue-basic fuchsin after Bennett *et al.* (1976). The epidermis was examined with an AMR 1000 scanning electron microscope after fixation and preparation following Dobbs' (1974) methodology.

Results

Stage duration and length of gestation

Length of time spent at each stage of development was determined from samples of embryos which were taken at intervals throughout gestation. Twenty-two samples from 8 fish provided 11 estimates to establish the relation between stage duration (D), measured in days/stage, and stage (S), which presented the midpoint of development stage between two sample intervals:

$$D = 0.0452S^{1.090}, \qquad n = 11, \qquad r^2 = 0.89$$

This relationship was nearly linear, with stage duration increasing with increasing stage number (Fig. 1). From the model of stage duration, a cumulative age of the embryo (time since fertilization) was calculated for stages 1 to 32 and plotted as a function of Oppenheimer developmental stage (Fig. 1). From stage 32 (estimated from the model to be reached in 31.2 days) to parturition, an average of 5.8 days elapsed for the 11 females in the study. The average gestation period at 10°C is therefore estimated to be 37 days. This agrees closely with our estimates from gestation periods of three individual fish which ovulated and were fertilized in the laboratory ($n = 3$, $x = 36.3$ days, $S = 0.58$).

Oxygen consumption rates

Embryonic *S. melanops* representing seven stages of development from eight females were used to determine total oxygen consumed during gestation. Depending upon stage of development, between 24 and 229 embryos were placed in each 15 ml respirometer flask. Embryos were judged to be inactive in respirometer flasks, but we could not observe activity during shaking of the flasks. Oxygen consumption

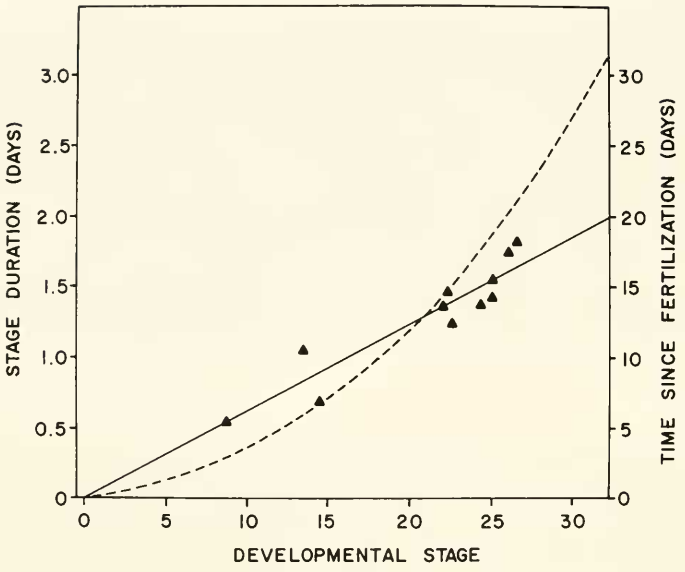

FIGURE 1. Duration of developmental stages during gestation of embryonic *Sebastes melanops* at 10°C. Developmental stages are determined according to Oppenheimer (1937). Stage durations (solid line) were estimated by successive catheterization of gestating females. The time since fertilization (dashed line) is an integration of the curve for stage duration; we estimate approximately 32 days to stage 32 and an additional 5 days until birth.

(μl/embryo/h) increased as embryonic development progressed (Fig. 2). The lowest oxygen uptake, averaging 0.0078 O_2/embryo/h, was measured from embryos in the earliest stage of development (stage 9 and approximately 2.4 days after fertilization as estimated from the stage duration model). The oldest embryos (stage 30 and 27.4 days after fertilization) utilized an average of 0.087 μl O_2/embryo/h. Oxygen consumption (Q, μl O_2/embryo/h), expressed as a function of time since fertilization (t, in days), is described by the equation:

$$Q = 0.00321t^{1.0026}, \qquad n = 8, \qquad r^2 = 0.98 \qquad \text{(Fig. 2)}.$$

From this curve a cumulative estimate of oxygen required over the estimated gestation period of 37 days was determined to be 54.667 μl O_2/embryo. Using an oxycaloric equivalent of 0.005 cal/μl O_2 (Lasker, 1962), the catabolic component of energy used during gestation would correspond to 0.273 calorie.

Energy and protein changes during development

Measurements of weight and caloric content for developing embryos are presented in Table I. Eight stages are represented, including unfertilized eggs just prior to ovulation and the extruded larvae. In general, both weight and caloric content gradually decreased throughout development. The AFDW of an unfertilized egg was 67.5 μg. From the CHN analysis, percent carbon and nitrogen were determined and caloric content was estimated to be 0.429 calorie/egg. A correction was made for caloric contribution by the chorion to total available energy, since the chorion provides no energy to the embryo. The average chorion AFDW of 1.11 μg was converted to a caloric value of 0.005 calorie, assuming 50% carbon content. The available energy to the embryo is

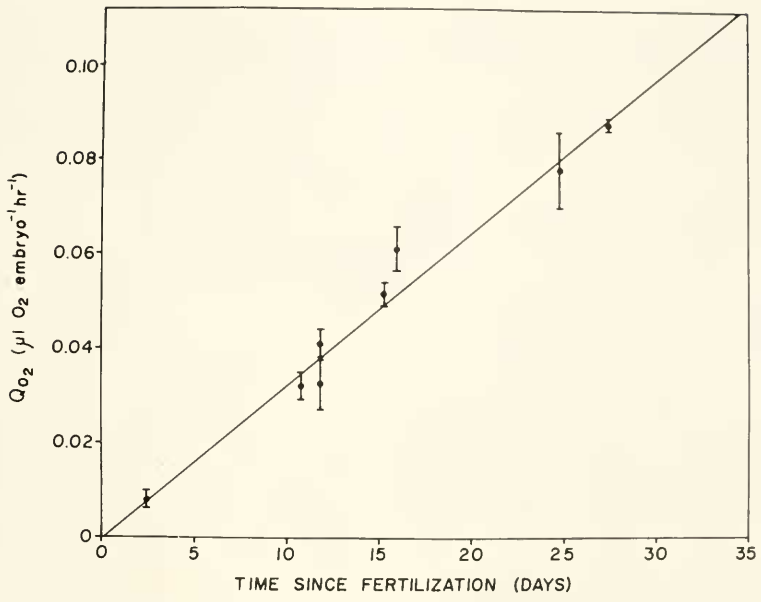

FIGURE 2. Oxygen consumption (μl O_2 embryo^{-1} h^{-1}) for embryonic *Sebastes melanops* as a function of time since fertilization at 10°C. Each point represents the mean of two to three observations on embryos from the same female; scale bars represent ±2 S.E.

therefore 0.424 calorie. At hatching, when the relatively well-developed larva still has a remnant of yolk, caloric measurements suggest that 81% of the initial egg energy remains in yolk and embryonic tissue. Nitrogen increases as a percentage of embryo dry weight with increasing time since fertilization, but this is balanced by decreasing total weight such that total nitrogen remains static (Table I; n = 12, r = −0.23, $P > 0.10$). Carbon, on the other hand, actually decreases with development (Table I; n = 12, r = −0.92, $P < 0.01$).

TABLE I

Weight, carbon, nitrogen, and caloric values of Sebastes melanops *embryos throughout gestation*

Oppenheimer stage	Dry weight embryo (μg)	AFDW embryo (μg)	Nitrogen (μg)	Carbon (μg)	C/N	Caloric content of embryo (cal/embryo)	Caloric content (embryo-chorion)
Nonfertilized egg	71	67.5	7.0	40.2	5.74	0.429	0.424
13	74	70.3	7.4	41.2	5.57	0.435	0.430
16	70	66.2	7.4	38.6	5.22	0.407	0.402
18	70	65.8	7.3	37.7	5.16	0.394	0.389
22	66	61.1	7.1	35.0	4.93	0.365	0.360
28	71	65.3	6.9	35.8	5.19	0.365	0.360
31	70	63.9	7.2	33.3	4.63	0.330	0.325
Larvae at birth	66.7	60.4	7.0	33.6	4.80	0.345	0.345

Developmental stages are determined after Oppenheimer (1937). (C/N = carbon to nitrogen ratio; AFDW = ash-free dry weight.)

If nonprotein nitrogen remained constant over development, total protein would remain static. In the 1984 examples, however, although the nitrogen remained static, protein decreased significantly during development ($n = 24$, $r = -0.73$, $P < 0.01$; Table II). These data suggest that nonprotein nitrogen increases from 1% in the earliest embryos studied to 27% in newly extruded larvae. This seems unusual in light of other values for teleosts, which range from 9 to 18% of total nitrogen (Niimi, 1972), and may be indicative of a nitrogenous source of maternal nutrition.

Comparing calorimetry and catabolic energy utilization provides evidence that additional maternal nutrition is provided during gestation. Based upon the calculation of 0.273 catabolic caloric necessary during gestation, 64.3% of the initial energy is used for catabolism. This suggests that the efficiency of yolk utilization from fertilization to parturition is approximately 36%. Calorimetry, however, shows that 81% of the initial energy investment remains at parturition. The difference represents energy from the maternal system. It is probable that the nutritional substance is nitrogenous, such as amino acids or peptides, since the total nitrogen remains nearly constant during gestation (Tables I, II). Comparing the time course of gestation and the energy content remaining as calculated by catabolism and calorimetry reveals the approximate times and developmental stages at which the nutrition is provided (Fig. 3). Energy content remaining after catabolism continued to decrease over development; measurements from calorimetry are similar through an embryonic age of about 20–25 days, corresponding to Oppenheimer stage 26.

The location of uptake of nutritional substances by embryonic *S. melanops* was approached from a structural standpoint, with examination of the epidermal surfaces and the histology of the alimentary tract. Epidermal uptake has been suggested for certain species and has been documented in the clinid *Clinus superciliosus* by Veith (1980). In embryonic *S. melanops,* we examined epidermal tissues at Oppenheimer stages 21, 31, and in larvae shortly after parturition, representing approximately 13, 29, and 38 days post-fertilization, respectively. At stage 21, prior to provision of maternal nutrients (Fig. 3), the epidermis on the nape (posterior to the cranium) and yolk sac regions is relatively smooth, with only cell boundaries distinct. Small, 3–4 μm depressions are apparent irregularly over the epidermis; these depressions may represent the locations of subdermal sacciform cells (Bullock, 1980). Only weak evidence of microridges, and no microvilli, are present (Fig. 4a). Epidermal microridges on stage 31 embryos are better developed in both nape (Fig. 4b) and yolk sac regions (Fig. 4c). In both of these developmental stages, relative development of the microridges decreases towards the tail. Finally in larvae shortly after birth, the microridges remain but are less distinct (Fig. 4d).

TABLE II

Comparison of protein, nitrogen, and carbon content from embryonic Sebastes melanops

Oppenheimer stage	Nitrogen (μg)	Carbon (μg)	Protein (μg)	PN/TN
9	7.30 (—)	41.64 (—)	45.27 (1.20)	0.99
23	7.78 (0.26)	40.71 (1.18)	46.27 (3.97)	0.95
28	7.64 (0.04)	38.48 (0.16)	36.23 (1.53)	0.76
Larvae at birth	7.74 (0.06)	34.42 (0.09)	35.31 (3.80)	0.73

Protein was determined using the methods of Itzhaki and Gill (1964) and carbon-nitrogen by CHN analyzer. Numbers in parentheses indicate one standard deviation. (PN/TN = ratio of protein nitrogen to total nitrogen.)

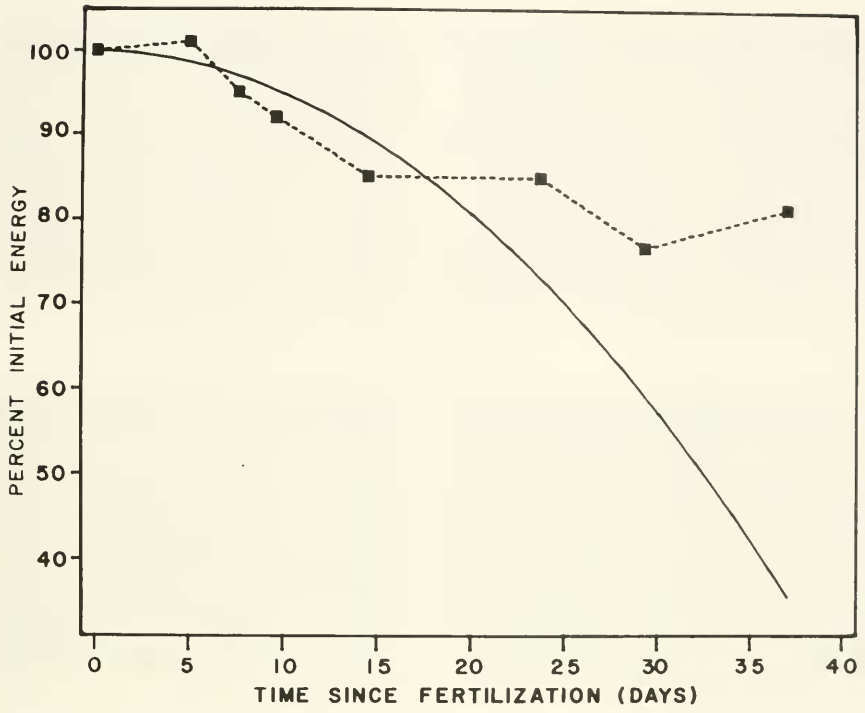

FIGURE 3. Comparison of energy budgets in embryonic *Sebastes melanops* during gestation based upon direct and indirect calorimetry. The dashed line represents caloric values of embryos at various times during gestation. The solid line represents energy utilization based upon the model of oxygen consumption during gestation and assumes an oxycalorific equivalent of 0.005 cal $(\mu l\ O_2)^{-1}$.

Histological observations on the gut of embryonic *S. melanops* demonstrate a change with increasing development. In early embryos, the foregut is not open, and the gut epithelium is relatively narrow and basophilic, with material lacking in the gut lumen (Fig. 5a). With development past stage 27, however, observation of whole embryos and serial sections show that the gut is open. Few histological changes are noted in either foregut or midgut regions, with the obvious exception of acidophilic material in the lumen (Fig. 5b). In the hindgut or rectum, however, the gut lumen also contains an amorphous substance and the height of the hindgut epithelium is greater. Additionally, there are large, supranuclear inclusions and some vacuolation (Fig. 5c). Finally, at stage 31, the hindgut epithelium is greatly expanded with marked increases of acidophilic supranuclear inclusions (Fig. 5d).

DISCUSSION

The reproductive mode in *Sebastes* has previously been termed "primitive" ovoviviparity (Amoroso, 1960; Wourms and Bayne, 1973; Wourms, 1981) despite a lack of experimental studies on this genus. The high fecundity, lack of structural modifications for embryonic nutrition, and small embryonic and larval size suggested that embryos received no nutrition beyond oogenesis. Our approach in this study has followed several studies on yolk utilization in oviparous species, and therefore comparisons of energy utilization are relevant here. Values useful for such comparisons

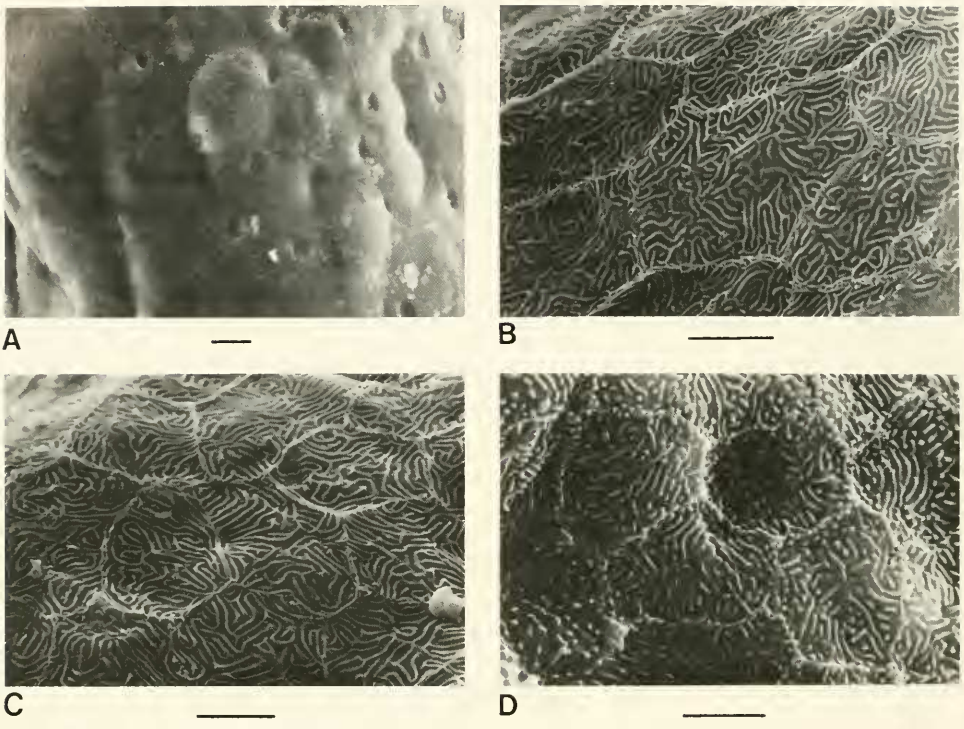

FIGURE 4. Scanning electron micrographs of the epidermis of embryonic and larval *Sebastes melanops*. a. Stage 21 embryo (13 days post-fertilization), nape region. Note the 3–4 μm depressions. Although the cell boundaries are distinct, the microridges are only poorly developed. b. Stage 31 embryo (29 days post-fertilization), nape region. c. Stage 31 embryo, yolk sac region. d. Larva shortly after parturition, nape region. Scale bars indicate 10 μm.

are the "plastic efficiency coefficient" (PEC) of Gray (1928) and the "apparent energetic efficiency" (AEE) of Needham (1931). The former is the ratio of dry weight of the developed embryo to that of yolk at fertilization, and the latter is the ratio of the caloric values of the same stages. Value of PEC and AEE from oviparous teleosts range from 0.24 to 0.65 and 0.26 to 0.79, respectively, and clearly demonstrate the expected decrease in mass and energy content during development (Table III). Among viviparous species, Thibault and Schultz (1978) noted values of PEC from 0.61 to 18.83 within the genus *Poeciliopsis;* their data suggest that *P. monacha* is a lecithotrophe, whereas the other three species receive varying levels of additional maternal nutrition during gestation.

Development in *Sebastes* shows some similarities to that in oviparous species. Oxygen consumption continually increases during gestation (Fig. 2), but the length of gestation is much greater than incubation time of equivalent sized eggs from oviparous species. Ware (1975), for example, compiled information on incubation times, sizes, and temperatures of marine species with pelagic eggs and demonstrated a highly significant relationship of egg diameter and incubation time. This relationship predicts an incubation time of 1.3 days given the egg size of *S. melanops* or an egg size of 4.4 mm given its incubation time; this is in marked contrast to the 37-day incubation and 0.8 mm egg size. The pattern of energy utilization described above also demonstrates important differences. The only prior information on *Sebastes,*

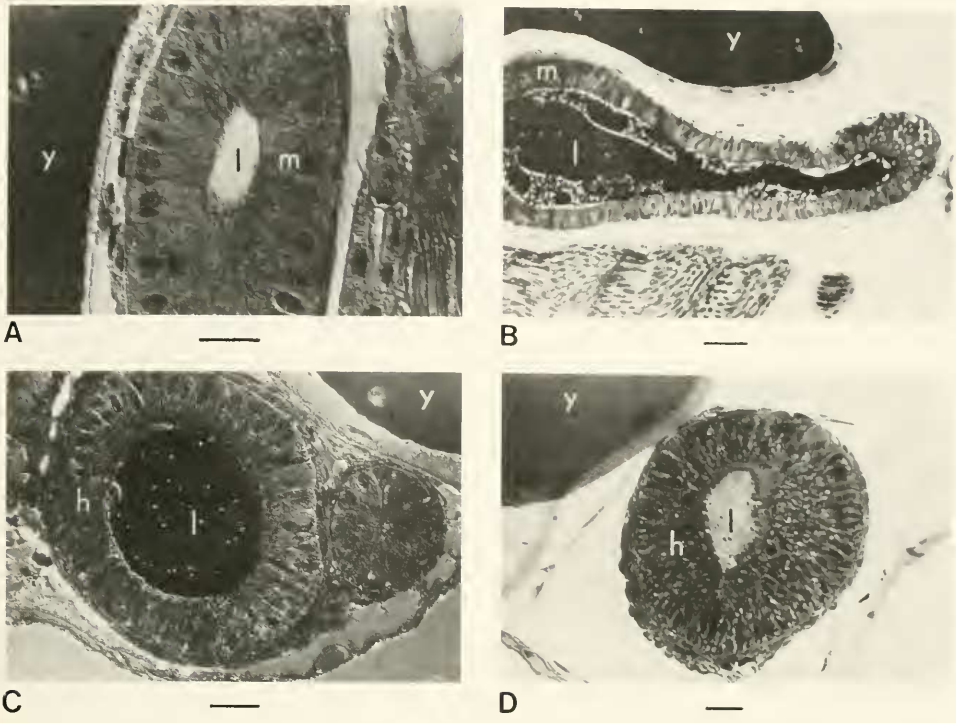

FIGURE 5. Histological sections of gut tissue in various stages of embryonic *Sebastes melanops*. a. Stage 21 embryo (13 days post-fertilization), midgut region dorsal to the yolk sac. Note the columnar gut epithelium and empty lumen (scale bar = 20 μm). b. Longitudinal section of the midgut-hindgut region of a stage 28 embryo (24 days post-fertilization). Note the densely staining, acidophilic substance throughout the lumen of the gut (scale bar = 50 μm). c. Cross section of the hindgut of a stage 28 embryo. Note the expanded hindgut epithelium with material in the lumen (scale bar = 20 μm). d. Cross section of the hindgut of a stage 31 embryo (29 days post-fertilization). The lumen contains an amorphous, granular substance, and the epithelial cells are characterized by supranuclear granules (scale bar = 20 μm). (h = hindgut epithelium; l = lumen; m = midgut epithelium; y = yolk sac.)

that of Hsaio (unpubl.), however, supports the idea of lecithotrophic viviparity in *S. marinus*. He demonstrated ". . . a pronounced fall in the dry weight of the developing egg, indicating little or no maternal contribution" (Needham, 1942). The only accessible data of Hsaio, however, are presented in Scrimshaw (1945), where the dry weight of the newly fertilized egg is presented as 0.003 g. This value is more than an order of magnitude greater than dry weights observed in the present study (Table I), and in Moser (1967a), which are in the range of 70–100 g. While the egg size in *S. marinus* is slightly larger than that of some Pacific species (Taning, 1961), it is doubtful that it could be 30-fold greater in dry weight. We therefore consider his unpublished values unreliable. Our value for PEC, 0.90, could conceivably be at the upper range of oviparous or lecithotrophic viviparous species (Table III). Furthermore, the value of AEE determined by oxgyen consumption is within the range of values determined for oviparous species. Relative to other species where both values are available, however, the relationship of the two values is inconsistent with the interpretation of lecithotrophic viviparity. Calorimetry demonstrates that the caloric content of the larva at parturition represents 81% of the initial energy invested at oogenesis. This value is more representative of that expected given the value of 0.90 for PEC. The sum of energy used

TABLE III

Efficiency of yolk utilization in selected fishes

	Temperature °C	PEC	AEE	Source
Oviparous species				
Tautoga onitis	16	0.41	0.36	Laurence, 1973
	19	0.29	0.26	Laurence, 1973
	22	0.30	0.26	Laurence, 1973
Congiopodus leucopaecilus	11.5	—	0.64	Robertson, 1974
Solea solea	10	—	0.68	Fluchter and Pandian, 1968
	15	—	0.55	Fluchter and Pandian, 1968
	20	—	0.47	Fluchter and Pandian, 1968
Limanda ferruginea	4–12	0.24–0.45	0.32–0.41	Howell, 1980
Paralichthys dentatus	16	0.61	0.62	Johns and Howell, 1980
Sardinops caerulea	14	0.48	0.79[1]	Lasker, 1962
Viviparous species				
Poeciliopsis monacha	22–32	0.61	—	Thibault and Schultz, 1978
P. lucida	22–32	1.34	—	Thibault and Schultz, 1978
P. prolifica	22–32	3.50	—	Thibault and Schultz, 1978
P. turneri	22–32	18.83	—	Thibault and Schultz, 1978
Sebastes marinus	—	0.66	—	Hsiao, unpub. (cited in Schrimshaw, 1945)
S. melanops	10	0.90	0.81 (0.36)[1]	Present study

PEC refers to the "plastic efficiency coefficient" (Gray, 1928) which is the ratio of dry weight of the developed embryo to that of the fertilized egg. AEE refers to the "apparent energetic efficiency" of Needham (1931), which is the same ratio using caloric values rather than dry weight. Values for viviparous species refer to embryos at parturition, when a small amount of yolk may remain.

[1] Utilization is based upon oxygen consumption and oxycalorific equivalents.

for catabolism (0.273 calorie) and that remaining at birth (0.345 calorie) represents 1.46 times that initially available at fertilization. A comparison of energy utilization during embryogenesis (Fig. 3) suggests that energy is first provided between Oppenheimer stages 22 and 28, corresponding to approximately 15 and 24 days after fertilization, respectively.

Viviparous teleosts display several adaptations for embryonic nutrition; the range of variation has been discussed in reviews on viviparity in fishes (Amoroso, 1960; Wourms, 1981). The most notable adapations for nutrient exchange are generally present in the embryonic, rather than maternal tissues. In some species, transfer of materials and respiratory gases may simply take place across the epithelium of the body and fins (Veith, 1979, 1980). In the embiotocids, the median fins become spatulate and highly vascularized, serving the function of respiratory gas exchange (Webb and Brett, 1972; Dobbs, 1975). Trophotaeniae are extensions of gut tissue present in several viviparous families which serve an absorptive function (Turner, 1937; Amoroso, 1960; Wourms and Cohen, 1975). These structures are continuous with the gut and assimilate ovarian secretions or histotrophe; similarly, other species may simply ingest ovarian fluid without externally specialized trophotaeniae (Dobbs, 1975; Veith, 1980).

In *S. melanops* embryos there are no notably specialized structures for uptake of histotrophe equivalent to those of more advanced viviparous species (Wourms and Bayne, 1973; Wourms, 1981). The epidermal structure of *S. melanops* embryos (Fig. 4) suggests that uptake does not occur there. Although there are numerous microridges

which generally characterize teleost epidermis (Yamada, 1968; Depeche, 1973; Roberts *et al.,* 1973), microvilli usually characterize the absorptive surfaces on embryos of viviparous fishes, both on epidermal (Veith, 1980) and trophotaenial surfaces (Lombardi and Wourms, 1978). Veith (1980), for example, noted numerous epidermal microvilli situated on macroridges in early embryos of *Clinus superciliosus* and demonstrated uptake of labeled compounds via autoradiography. Uptake was limited to relatively small embryos, however, as the microvilli fused to form epidermal microridges later in gestation when the gut assumed the function of nutrient uptake. In *S. melanops,* the increased development of microridges with time after fertilization (Fig. 4) may be a response to increased oxygen consumption (Fig. 2), even after parturition, since larval fish epidermis often serves a respiratory function (Weihs, 1980).

The other possible site of nutrient uptake is the gut. Examination of gross morphology of embryos during gestation demonstrates that the mouth is open and the gut continuous at Oppenheimer stage 27, approximately 22 days post-fertilization. This time correlates well with the timing of maternal nutrition as estimated in Figure 3. Histological examination of the gut agrees with this assessment (Fig. 5). In early stage embryos, the gut epithelium is relatively narrow and basophilic (Fig. 5a), a condition similar to that described by Govoni (1980) for nonfeeding yolk sac larvae of *Leiostomus xanthurus.* With development past stage 27 in embryonic *S. melanops,* however, an amorphous acidophilic material is present in the lumen of the hindgut, evidence of ingestion of histotrophe (Fig. 5b, d); this may be similar to the material observed in the expanded hindgut of stage 28 *S. schlegeli* by Shimizu and Yamada (1980). This material is absent in earlier stages. Also the most marked change in the gut epithelium occurs in the hindgut, where the epithelium is characterized by marked expansion and development of supranuclear acidophilic inclusions and vacuolation (Fig. 5d). O'Connell (1976), in diagnosing the feeding condition of larval *Engraulis mordax,* used similar supranuclear, eosinophilic inclusion bodies in the hindgut to evaluate the relative nutritional state of larvae. Actively feeding larvae were characterized by "massive" supranuclear inclusions in the hindgut; his histological figures of this state are similar to those of later stage embryos of *S. melanops.*

Evidence for uptake of exogenous substances in the hindgut supports the idea that the substance is possibly amino acids, peptides, or proteins. Iwai (1969) suggested that protein is absorbed in the hindgut of larval fishes, largely by pinocytosis. This has been confirmed by Watanabe (1981, 1982), who described the uptake and intracellular digestion of horseradish peroxidase in the guts of larvae of several teleosts. The nitrogen content of developing embryos of *S. melanops* remains nearly constant (Table I) while protein decreases (Table II). In development of most oviparous teleost larvae, protein and nitrogen decrease during development. Rogers and Westin (1981) noted a decrease of 48% in total nitrogen in developing striped bass larvae and a marked increase in the carbon:nitrogen ratio, which contrasts with the decreasing ratio in *S. melanops* (Tables I, II). Similarly, Hayes (1949) suggested that 40% of the original yolk proteins in the trout egg are used as energy sources in development. Thus while other sources of nutrition cannot be ruled out, protein or other nitrogenous energy sources are clearly involved in additional maternal nutrition of embryos.

Although the basic reproductive pattern in the genus *Sebastes* is similar among species, variations in reproductive strategy and life history pattern exist. Variations in maximum size (and therefore fecundity), age at maturity, seasonality of spawning, multiple spawning, and longevity are well documented within the genus; furthermore, intraspecific variations may occur with latitude (Boehlert and Kappenman, 1980). Small species such as *Sebastes jordani* and *S. emphaeus* may mature at age 2, reach a maximum size of 179 mm (*S. emphaeus*) and maximum ages of about 7 years,

and achieve maximum fecundity of approximately 50,000 developing embryos (Phillips, 1964; Moulton, 1975). Larger species such as *S. paucispinis* may mature at age 4 or later, reach maximum lengths of 870 mm, bear an annual or biannual brood of up to 2,300,000 developing embryos, and reach maximum ages of 30 years (Phillips, 1964; Moser, 1967a). Other investigators have documented ages greater than 80 years (Bennett *et al.*, 1982). Other species have not been studied relative to additional maternal contribution. The opaque substance in the enlarged rectum of *S. schlegeli* embryos noted by Shimizu and Yamada (1980), however, suggests a similar nutritional mode during gestation. Ultrastructural analysis of rectal cells of embryos in this species reveals that they are characterized by supranuclear inclusions similar to those noticed in *S. melanops* (Fig. 5d), also indicative of exogenous nutrition (M. Shimizu, pers. comm.). Thus the pattern of nutrition documented for *S. melanops* may occur in other species in this genus. Given the wide variety of over 100 species of *Sebastes* (Barsukov, 1981), however, there may be variability in maternal nutrition as is apparent within genera of other viviparous groups such as the poeciliids (Table III; Thibault and Schultz, 1978).

Viviparity in *Sebastes* is a significant adaptation to environmental conditions, as in other viviparous species (Amoroso, 1960; Wourms, 1981). Although Turner (1947) could draw no ecological correlations with reproductive type among the poeciliids, Thibault and Schultz (1978) suggested that the diverse reproductive mechanisms relate closely to conditions of predators, food availability, and physical environment. In marine fishes, most mortality is concentrated in the early life history during so-called "critical periods" (Hjort, 1914; Marr, 1956). In the Pacific sardine, for example, mortality may be 30% per day during the pelagic egg stage (Smith, 1973) and 10% per day during the larval stage (Lenarz, 1973). Thus brooding of embryos during development may significantly decrease early mortality due to predation and starvation. Further, less energy is necessary for protection of the embryo. In oviparous species, the chorion represent 15–33% of egg dry weight (Blaxter and Hempel, 1966; Robertson, 1974); in *S. melanops,* however, it represents only 1.6%. The protective function served by the chorion in oviparous species (Davenport *et al.*, 1981) is apparently unnecessary in the benign ovarian environment. The chorion in *S. paucispinis* embryos is only 1 μm thick and "porous" in nature (Moser, 1967b). It is probable that this chorion does not prevent movement of macromolecules, since exogenous nutrition of embryonic *S. melanops* occurs some 8 days prior to hatching from the chorion.

Within the family Scorpaenidae, seven of eight subfamilies are oviparous; only the Sebastinae is characterized by internal fertilization and viviparity. *Sebastes* is clearly the most advanced genus within this group, which also includes the genera *Hozukius* and *Helicolenus.* While the reproductive pattern of the deep-living *Hozukius* is unknown (Barsukov, 1981), *Helicolenus* is thought to be the most primitive (Krefft, 1961). While internally fertilized, *Helicolenus* lays gelatinous egg masses similar to those of the oviparous genera *Scorpaena* and *Sebastolobus;* larvae at parturition are in varying stages of development (Krefft, 1961; Graham, 1939). In the genus *Sebastiscus* (considered a subgenus of *Sebastes* by Barsukov and Chen, 1978) parturition occurs immediately after hatching in the ovary (Tsukahara, 1962). There has been some controversy concerning the stage of development at birth in *Sebastes,* but observations of natural birth generally support hatching within the ovary (Moser 1967b; Kusakari, 1978; present study). We estimate that 5 days elapse between hatching and birth for *S. melanops* at 10°C.

While *Sebastes* is the most reproductively advanced genus within the Scorpaenidae, it is generally considered primitive among viviparous fishes (Amoroso, 1960; Wourms, 1981). A primitive character present in the *Sebastes* female reproductive system is

the presence of paired ovaries which are uncommon among viviparous species (Amoroso, 1960). A unique specialization in the reproductive system is the dual arterial system supplying fresh arterial blood to each ovary, which no doubt presents a relatiely high respiratory oxygen demand on the maternal system during embryogenesis (Moser, 1967b). It is interesting to note that the genera of the subfamily Sebastinae show morphological and osteological evidence for primitive and advanced characters which correspond to the degree of reproductive specialization; *Helicolenus* is most primitive and closest to the ancestral, oviparous scorpaenines, *Sebastes* is the most advanced (Krefft, 1961; Moser and Ahlstrom, 1978).

Kusakari *et al.* (1977) observed that the larvae of *S. schlegeli* at spawning are embedded in a gelatinous matrix which gradually dissolves after pectoral fanning by the female. Such a gelatinous substance is consistent with the gelatinous egg masses of *Helicolenus, Scorpaena,* and *Sebastolobus.* Wourms (1981) questioned whether this jelly in *Helicolenus* might play some trophic function. We have not observed spawning or such a viscous matrix in *S. melanops;* thus ovarian fluid may be a more fluid histrophe in this species. This histotrophe may be produced in the granulosa cells noted by Moser (1967b) to hypertrophy in *S. paucispinis* ovaries. A second source of histotrophe may arise from resorbed embryos which die during development. Boehlert *et al.* (1982) observed degenerating embryos in fertilized *S. entomelas* ovaries and noted decreased fecundity with later developmental stages in this species. In the latter case, if embryonic death occurs, the energy contained in these embryos may be recovered by brood mates.

Reproductive similarities among genera in the subfamily Sebastinae and relationships with other genera in the family suggest that evolution of viviparity proceeded through progressively longer retention of developing embryos. In the ancestor of extant sebastines, internal fertilization was probably followed by rapid deposition of fertilized embryos (Barsukov, 1981), a condition termed ovi-ovoviviparity by Balon (1975). In *Helicolenus* retention time of fertilized embryos may be variable (Krefft, 1961), with eggs deposited shortly after fertilization, or retained for longer periods (Graham, 1939). *Sebastes* larvae, on the other hand, are typically ready to feed at birth, with organogenesis complete. Thus evolution of viviparity in the scorpaenids involved progressively greater commitments of parental care; additional nutrition from ovarian fluid, or histotrophe, may have simply developed as an "opportunistic and passive strategy" (Wourms, 1981). It would thus be interesting to investigate the range of variability in viviparity for the genus *Sebastes.*

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LITERATURE CITED

AHLSTROM, E. H. 1961. Distribution and relative abundance of rockfish (*Sebastodes* spp.) larvae off California and Baja California. *Rapp. P. V. Reun. Cons. Perm. Int. Explor. Mer* **150**: 169–176.

AMOROSO, E. C. 1960. Viviparity in fishes. *Symp. Zool. Soc. Lond.* **1**: 153–181.

BALON, E. K. 1975. Reproductive guilds of fishes: A proposal and definition. *J. Fish. Res. Board Can.* **32:** 821–864.

BARSUKOV, V. V. 1981. A brief review of the subfamily Sebastinae. *J. Ichthyol.* **21:** 1–26.

BARSUKOV, V. V., AND L. C. CHEN. 1978. Review of the subgenus *Sebastiscus* (*Sebastes, Scorpaenidae*) with a description of a new species. *Vopr. Ikhtiol.* **18:** 195–210.

BENNETT, H. S., A. D. WYRICK, S. W. LEE, AND J. H. MCNEIL, JR. 1976. Science and art in preparing tissues embedded in plastic for light microscopy, with special reference to glycol methacrylate, glass knives, and simple stains. *Stain Technol.* **51:** 79–97.

BENNETT, J. G., G. W. BOEHLERT, AND K. K. TUREKIAN. 1982. Confirmation of longevity in *Sebastes diploproa* (Pisces: Scorpaenidae) using $^{210}PB/^{226}Ra$ measurements in otoliths. *Mar. Biol.* **71:** 209–215.

BLAXTER, J. H. S., AND G. HEMPEL. 1966. Utilization of yolk by herring larvae. *J. Mar. Biol. Assoc. U. K.* **46:** 219–234.

BOEHLERT, G. W., W. H. BARSS, AND P. B. LAMBERSON. 1982. Fecundity of the widow rockfish, *Sebastes entomelas,* off the coast of Oregon. *Fish. Bull. (U.S.)* **80:** 881–884.

BOEHLERT, G. W., AND R. F. KAPPENMAN. 1980. Variation of growth with latitude in two species of rockfish (*Sebastes pinniger* and *S. diploproa*) from the northeast Pacific Ocean. *Mar. Ecol. Prog. Ser.* **3:** 1–10.

BOEHLERT, G. W., AND M. M. YOKLAVICH. 1983. Effects of temperature, ration, and fish size on growth of juvenile black rockfish, *Sebastes melanops. Env. Biol. Fish.* **8:** 17–28.

BULLOCK, A. M. 1980. A comparative study of the epidermal morphology of fishes of the order anacanthinic with reference to their ecology and distribution. *Oceanogr. Mar. Biol. Annu. Rev.* **18:** 251–315.

DAVENPORT, J., S. LONNING, AND E. KJORSVIK. 1981. Osmotic and structural changes during early development of eggs and larvae of the cod, *Gadus morhua.* L. *J. Fish Biol.* **19:** 317–331.

DEPECHE, J. 1973. Intrastructure supervicielle de al vesicule vitellaire et du sac pericardique de l'embryon de *Poecilia reticulata* (Poisson Teleosteen). *Z. Zellforsch. Mitrosk. Anat.* **141:** 235–253.

DOBBS, G. H. 1974. Soft tissues of marine teleosts. Pp. 72–82 in *Principles and Techniques of Scanning Electron Microscopy,* M. Hayat, ed. Van Nostrand Reinhold Co., New York.

DOBBS, G. H. 1975. Scanning electron microscopy of intraovarian embyros of the viviparous teleost *Micrometrus minimus* (Gibbons), (Perciformes: Embiotocidae). *J. Fish Biol.* **7:** 209–214.

FINLAY, B. J., AND G. UHLIG. 1981. Calorific and carbon values of marine and freshwater protozoa. *Helgol. Wiss. Meeresunters.* **34:** 401–412.

FLUCHTER, J., AND T. J. PANDIAN. 1968. Rate and efficiency of yolk utilization in developing eggs of the sole *Solea solea. Helgol. Wiss. Meeresunters.* **18:** 53–60.

FORSTER, R. P., AND S. K. HONG. 1958. *In vitro* transport of dyes by isolated renal tubules of the flounder as disclosed by direct visualization: Intracellular accumulation and transcellular movement. *J. Cell. Comp. Physiol.* **51:** 259–272.

FUJITA, S. 1957. On the larval stages of a scorpaenid fish, *Sebastodes pachycephalus nigricans* (Schmidt). *Jpn. J. Ichthyol.* **6:** 91–93.

GOVONI, J. J. 1980. Morphological, histological, and functional aspects of alimentary canal and associated organ development in larval *Leiostomus xanthurus. Rev. Can. Biol.* **39:** 69–80.

GRAHAM, D. H. 1939. Breeding habits of the fishes of Otago Harbor and adjacent seas. *Trans. Proc. R. Soc. N. Z.* **69:** 361–372.

GRAY, J. 1928. The growth of fish. II. The growth rate of the embryo of *Salmo fario. J. Exp. Biol.* **6:** 110–124.

HART, J. L. 1973. Pacific fishes of Canada. *Fish. Res. Board Can. Bull.* **180:** 740 pp.

HAYES, F. R. 1949. The growth, general chemistry, and temperature relations of salmonid eggs. *Q. Rev. Biol.* **24:** 281–308.

HJORT, J. 1914. Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. *Rapp. P. V. Reun. Cons. Perm. Int. Explor. Mer* **20:** 1–228.

HOWELL, W. H. 1980. Temperature effects on growth and yolk utilization in yellowtail flounder, *Limanda ferruginea,* yolk-sac larvae. *Fish. Bull. (U.S.)* **78:** 731–740.

ITZHAKI, R. F., AND D. M. GILL. 1964. A microbiuret method for estimating proteins. *Anal. Biochem.* **9:** 401–410.

IWAI, T. 1969. Fine structure of gut epithelial cells of larval and juvenile carp during absorption of fat and protein. *Arch. Hist. Jpn.* **30:** 183–199.

JOHNS, D. M., AND W. H. HOWELL. 1980. Yolk utilization in summer flounder (*Paralichthys dentatus*) embryos and larvae reared at two temperatures. *Mar. Ecol. Prog. Ser.* **2:** 1–8.

KREFFT, G. 1961. A contribution to the reproductive biology of *Helicolenus dactylopterus* (De la Roche, 1809) with remarks on the evolution of the Sebastinae. *Rapp. P. V. Reun. Cons. Perm. Int. Explor. Mer* **150:** 243–244.

KUSAKARI, M. 1978. Pp. 117–139 in *Annual Report of the Hokkaido Institute of Mariculture.*

KUSAKARI, M. Y., O. MORI, AND K. KUDO. 1977. Studies on the breeding habit of a rock fish, *Sebastes schlegeli* (Hilgendorf). 2. On the breeding behavior of pregnant fish and the just spawned larvae. *J. Hokkaido Fish. Exp. Stn.* **34:** 1–11.

LAROCHE, W. A., AND S. L. RICHARDSON. 1980. Development and occurrence of larval and juveniles of the rockfishes *Sebastes flavidus* and *Sebastes melanops* (Scorpaenidae) off Oregon. *Fish. Bull. (U.S.)* **77:** 901–924.

LASKER, R. 1962. Efficiency and rate of yolk utilization by developing embryos and larvae of the Pacific sardine *Sardinops caerulea* (Girard). *J. Fish. Res. Board Can.* **19:** 867–875.

LAURENCE, G. C. 1973. Influence of temperature on energy utilization of embryonic and prolarval tautog, *Tautoga onitis*. *J. Fish. Res. Board Can.* **30:** 435–442.

LENARZ, W. H. 1973. Dependence of catch rates on size of fish larvae. *Rapp. P. V. Reun. Cons. Perm. Int. Explor. Mer* **164:** 270–275.

LOMBARDI, J., AND J. P. WOURMS. 1978. SEM of trophotaeniae, embryonic adaptations in an ophidioid, *Microbrotula randalli* and other viviparous fishes. *Am. Zool.* **18:** 607.

MACGREGOR, J. S. 1970. Fecundity, multiple spawning, and description of the gonads in *Sebastodes*. *U. S. Fish Wildl. Serv., Spec. Sci. Rep. Fish.* **596:** 12 pp.

MARR, J. C. 1956. The "critical period" in the early life history of marine fishes. *J. Cons. Perm. Int. Explor. Mer* **21:** 160–170.

MCCLURE, R. E. 1982. Neritic reef fishes off central Oregon: Aspects of life histories and the recreational fishery. M.S. Thesis, Oregon State University, Corvallis, Oregon.

MOSER, H. G. 1967a. Reproduction and development of *Sebastodes paucispinnis* and comparison with other rockfishes off Southern California. *Copeia* **1967:** 773–797.

MOSER, H. G. 1967b. Seasonal histological changes in the gonads of *Sebastodes paucispinnis* Ayres, an ovoviviparous teleost (Family Scorpanidae). *J. Morphol.* **123:** 329–354.

MOSER, H. G., AND E. H. AHLSTROM. 1978. Larvae and pelagic juveniles of blackgill rockfish, *Sebastes melanostomus*, taken in midwater trawls off southern California and Baja California. *J. Fish. Res. Board Can.* **35:** 981–996.

MOSER, H. G., E. H. AHLSTROM, AND E. M. SANDKNOP. 1977. Guide to the identification of scorpionfish larvae (Family Scorpaenidae) in the eastern Pacific with comparative notes on species of *Sebastes* and *Helicolenus* from other oceans. *NOAA Tech. Rep. NMFS CIRC*-**402,** 71 pp.

MOSER, H. G., AND J. L. BUTLER. 1981. Description of reared larvae and early juveniles of the calico rockfish, *Sebastes dalli* (Eigenmann and Beeson 1894). *CalCOFI Rep.* **2:** 88–95.

MOULTON, L. L. 1975. Life history observations of the Puget Sound rockfish *Sebastes emphaeus* (Starks 1911). *J. Fish. Res. Board Can.* **32:** 1439–1442.

NEEDHAM, J. 1931. *Chemical Embryology.* Cambridge, England. 2021 pp.

NEEDHAM, J. 1942. *Biochemistry and Morphogenesis.* Cambridge Univ. Press, London and New York. 787 pp.

NIIMI, A. J. 1972. Total nitrogen, nonprotein nitrogen, and protein content in largemouth bass (*Micropterus salmoides*) with reference to quantitative protein estimates. *Can. J. Zool.* **50:** 1607–1610.

O'CONNELL, C. P. 1976. Histological criteria for diagnosing the starving condition in early post yolk sac larvae of the northern anchovy, *Engraulis mordax* Girard. *J. Exp. Mar. Biol. Ecol.* **25:** 285–312.

OPPENHEIMER, J. M. 1937. The normal stages of *Fundulus heteroclitus*. *Anat. Rec.* **68:** 1–15.

PHILLIPS, J. B. 1964. Life history studies on ten species of rockfish (genus *Sebastodes*). *Calif. Dep. Fish Game Fish Bull.* **126:** 70 pp.

ROBERTS, R. J., M. BELL, AND H. YOUNG. 1973. Studies on the skin of plaice (*Pleuronectes platessa* L.) II. The development of larval plaice skin. *J. Fish Biol.* **5:** 103–108.

ROBERTSON, D. A. 1974. Developmental energetics of southern pigfish (Teleostei: Congriopodidae). *N. Z. J. Mar. Freshwater Res.* **8:** 611–620.

ROGERS, B. A., AND D. T. WESTIN. 1981. Laboratory studies on effects of temperature and delayed initial feeding on development of striped bass larvae. *Trans. Am. Fish. Soc.* **110:** 100–110.

SALONEN, K., J. SARVALA, I. HAKALA, AND M. L. VILJANEN. 1976. The relation of energy and organic carbon in aquatic invertebrates. *Limnol. Oceanogr.* **21:** 724–730.

SCRIMSHAW, N. S. 1945. Embryonic development in poeciliid fishes. *Biol. Bull.* **88:** 233–246.

SHIMIZU, M., AND J. YAMADA. 1980. Ultrastructural aspects of yolk absorption in the vitelline syncytium of the embryonic rockfish, *Sebastes schlegeli*. *Jpn. J. Ichthyol.* **27:** 56–63.

SMITH, C. L., C. S. RAND, B. SCHAEFFER, AND J. W. ATZ. 1975. *Latimeria*, the living coelacanth, is ovoviviparous. *Science* **190:** 1105–1106.

SMITH, P. E. 1973. The morality and dispersal of sardine eggs and larvae. *Rapp. R. P. Reun. Cons. Perm. Int. Explor. Mer* **164:** 281–292.

SOROKIN, V. P. 1961. The redfish; gametogenesis and migrations of the *Sebastes marinus* (L.) and *Sebastes mentella* Travin. *Rapp. P. V. Reun. Cons. Perm. Int. Explor. Mer* **150:** 245–250.

TANING, A. V. 1961. Larval and postlarval stages of *Sebastes* species and *Helicolenus dactylopterus*. *Rapp. P. V. Reun. Cons. Perm. Int. Explor. Mer* **150:** 234–240.

THIBAULT, R. E., AND R. J. SCHULTZ. 1978. Reproduction adaptations among viviparous fishes (Cyprinidontiformes: Poeciliidae). *Evolution* **32:** 320–333.

TSUKAHARA, H. 1962. Studies on habits of coastal fishes in the Amakusa Islands. 2. Early life history of the rockfish *Sebastiscus marmoratus* (Cuvier et Valenciennes). *Rec. Oceanogr. Works. Jpn. Spec.* **6:** 49–55.

TURNER, C. L. 1937. The trophotaenidae of the Goodeidae, a family of viviparous cyprinodont fishes. *J. Morphol.* **61:** 495–523.

TURNER, C. L. 1947. Viviparity in teleost fishes. *Sci. Mon.* **65:** 508–518.

UMBREIT, W. W., R. H. BURRIS, AND J. F. STAUFFER. 1972. *Manometric and Biochemical Techniques.* Burgess Publ. Co., Minneapolis. 387 pp.

VEITH, W. J. 1979. The chemical composition of the follicular fluid of the viviparous teleost *Clinus superciliosus*. *Comp. Biochem. Physiol.* **63A:** 37–40.

VEITH, W. J. 1980. Viviparity and embryonic adaptations in the teleost *Clinus superciliosus*. *Can. J. Zool.* **58:** 1–12.

WARE, D. M. 1975. Relation between egg size, growth, and natural mortality of larval fish. *J. Fish. Res. Board Can.* **32:** 2503–2512.

WATANABE, Y. 1981. Ingestion of horseradish peroxidase by the intestinal cells in larvae of juveniles of some teleosts. *Bull. Jpn. Soc. Sci. Fish.* **47:** 1299–1307.

WATANABE, Y. 1982. Intracellular digestion of horseradish peroxidase by the intestinal cells of teleost larvae and juveniles. *Bull. Jpn. Soc. Sci. Fish.* **48:** 37–42.

WEBB, P. W., AND J. R. BRETT. 1972. Respiratory adaptations of prenatal young in the ovary of two species of viviparous seaperch, *Rhacochilus vacca* and *Embiotoca lateralis*. *J. Fish. Res. Board Can.* **29:** 1525–1542.

WEIHS, D. 1980. Respiration and depth control as possible reasons for swimming of northern anchovy, *Engraulis mordax*, larvae. *Fish. Bull. (U. S.)* **78:** 109–118.

WOURMS, J. P. 1981. Viviparity: The maternal-fetal relationship in fishes. *Am. Zool.* **21:** 473–515.

WOURMS, J. P., AND O. BAYNE. 1973. Development of the viviparous brotulid fish, *Dinematichthys illucoeteoides*. *Copeia* **1973:** 32–40.

WOURMS, J. P., AND D. COHEN. 1975. Trophotaeniae, embryonic adaptations in the viviparous ophidioid fish, *Oligopus longhursti:* A study of museum specimens. *J. Morphol.* **147:** 385–401.

WOURMS, J. P., M. D. STRIBLING, AND J. W. ATZ. 1980. Maternal fetal nutrient relationships in the coelacanth, *Latimeria*. *Am. Zool.* **20:** 962.

YAMADA, J. 1968. A study on the structure of surface cell layers in the epidermis of some teleosts. *Annot. Zool. Jpn.* **41:** 1–8.